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CAN TOWNSEND'S GROUND SQUIRRELS SURVIVE ON A DIET OF EXOTIC ANNUALS?

Eric Yensen[1] and Dana L. Quinney[2]

Abstract.—Southwestern Idaho desert shrub–bunchgrass rangeland is being invaded by fire-prone exotic annuals that permanently dominate the landscape following wildfires. This study was undertaken to describe diets of Townsend's ground squirrels (*Spermophilus townsendii idahoensis*) at four study sites with varying degrees of exotic annual invasion to determine if the squirrels could utilize high proportions of exotic annuals in their diets. Townsend's ground squirrels were collected in March and May of 1987 and 1988, and stomach contents were analyzed using a microhistological technique. Grasses comprised 37–87% of Townsend's ground squirrel diets at the four sites. Native species, especially Sandberg's bluegrass (*Poa secunda*), winterfat (*Ceratoides lanata*), big sagebrush (*Artemisia tridentata*) and six-weeks fescue (*Vulpia octoflora*) constituted 7–96% ($\bar{x}$ = 47.2%) of the diet, whereas exotic species, especially cheatgrass (*Bromus tectorum*), tumbleweed (*Salsola iberica*), and tansymustards (*Descurainia* spp.) made up 4–68% ($\bar{x}$ = 48.0%) of the diet. At each site 2–4 species comprised >90% of the diet. There was no apparent correlation between the importance values of exotic species at a site and their importance in Townsend's ground squirrel diets.

Key words: Spermophilus townsendii, *food habits, dietary analysis, Idaho, ground squirrels.*

The Snake River Birds of Prey Area is a 243,000-ha tract of multiple-use shrub-steppe rangeland administered by the U.S. Bureau of Land Management. Townsend's ground squirrels (*Spermophilus townsendii idahoensis*) are important prey of raptors, and continued existence of the area's dense breeding populations of raptors depends upon dense Townsend's ground squirrel populations (U.S. Department of Interior 1979).

Invasion of southwestern Idaho rangeland by exotic annuals such as cheatgrass (*Bromus tectorum*), tumblemustard (*Sisymbrium altissimum*), pinnate tansymustard (*Descurainia pinnata*), and tumbleweed (*Salsola iberica*) has resulted in frequent and destructive wildfires that kill native shrubs and weaken native bunchgrasses. Over time, fires have resulted in the permanent replacement of native shrub- and bunchgrass-dominated communities by exotic annual-dominated communities (Yensen 1980, Kochert and Pellant 1986).

Townsend's ground squirrel populations are much less stable in exotic annual-dominated communities than in native shrub communities (Yensen et al. 1992). Native perennial forbs, bunchgrasses, and shrubs apparently provide a more constant, stable food source than exotic annual species that may vary in productivity between wet and dry years by several orders of magnitude (Young et al. 1987).

Like other ground squirrels of subgenus *Spermophilus*, Townsend's ground squirrels eat green vegetation early in their four- to five-month active season, then eat seeds of grasses and forbs to fatten up for hibernation (Howell 1938, Rickart 1982). In southwestern Idaho, Townsend's ground squirrels are in estivation/hibernation from June or July until the following January or February with low survival rates (ca. 28%; Smith and Johnson 1985). Food quantity and quality could influence overwintering survival as well as reproductive success the following spring.

Townsend's ground squirrels are known to eat native forbs (*Sphaeralcea;* Davis 1939), bunchgrasses (*Poa* sp.; June grass, *Koeleria* sp.; Davis 1939), and desert shrubs (big sagebrush, *Artemisia tridentata;* budsage, *Artemisia spinescens;* shadscale, *Atriplex confertifolia;* Davis 1939, Johnson 1961), as well as insects such as grasshoppers and cicadas, and occasionally carrion

[1]Museum of Natural History, Albertson College, Caldwell, Idaho 83605
[2]Bureau of Land Management, 3948 Development Ave., Boise, Idaho 83705. Present address: Idaho Army National Guard, Department of Environment, Box 45, Gowen Field, Boise, Idaho 83705.

TABLE 1. Vegetation importance values (% relative cover plus % frequency) in May 1987 and 1988 at four study sites near Coyote Butte in the Snake River Birds of Prey Area, southwestern Idaho.

Species	Study Site							
	Big sagebrush		Native grasses		Exotic annuals		Rehabilitation seeding	
	1987	1988	1987	1988	1987	1988	1987	1988
GRASSES								
Bromus tectorum	25	2	11	33	86	35	0	31
Poa secunda	67	60	90	58	45	45	85	60
Vulpia octoflora	16	7	24	0	2	8	12	3
Sitanion hystrix	16	11	14	14	8	21	0	28
Agropyron desertorum	0	0	0	0	0	0	29	2
SHRUBS								
Ceratoides lanata	29	47	3	5	0	0	7	0
Artemisia tridentata	33	39	0	0	0	4	0	0
Atriplex nuttallii	0	0	0	0	0	0	0	20
FORBS								
Salsola iberica	0	0	33	26	0	0	40	18
Descurainia sophia	0	0	3	0	0	0	0	0
Sisymbrium altissimum	0	11	8	31	34	14	0	5
Lactuca serriola	0	0	0	0	0	0	4	0
Other forbs	0	5	0	9	0	2	0	2
TOTAL COVER (%)	35	24	26	15	21	10	18	14

*Exotic species

Howell 1938, Alcorn 1940). However, they do eat introduced cheatgrass, tumblemustard, peppergrass (*Lepidium perfoliatum*; Davis 1939) as well as crop species like alfalfa, wheat, barley, potatoes, beets, carrots, and lettuce (Howell 1938).

Johnson (1980) and Rogers and Gano (1980) studied diets of *Spermophilus townsendii townsendii* in Washington and found native bluegrass (*Poa* sp., 26–29%) and lupine (*Lupinus laxiflorus*, 11–25%) to be dietarily important, whereas *Descurainia* was the only exotic eaten in quantity (15–33%); cheatgrass, tumbleweed, tumblemustard, and peppergrass constituted 0–4% of the diet. Johnson et al. (1977) estimated the percent volume of food categories in 174 Townsend's ground squirrel stomachs in the Snake River Birds of Prey Area. They found grasses, including cheatgrass, were most important, followed by forbs and winterfat (*Ceratoides lanata*).

Because cheatgrass, tumbleweed, tumblemustard, and peppergrass are becoming increasingly dominant in the Snake River Birds of Prey Area, this study was designed to learn if Townsend's ground squirrels were substituting these exotics for native species in their diets. We also wished to learn if consumption-introduced plant species increased with increases in the proportion of exotic annual species in the habitat. However, the study was not designed to study dietary preference as such.

STUDY SITES

Four study sites were located near Coyote Butte, approximately 19 km south of Kuna, Ada County, Idaho, in the Snake River Birds of Prey Area. The sites described below were selected for progressively greater deviation from undisturbed native vegetation.

UNBURNED BIG SAGEBRUSH.—This site (T1S, R1W, Sec. 24; elev. 850 m) is a big sagebrush–winterfat mosaic and represents the unburned condition of the other three sites. Big sagebrush, winterfat, and native grasses (Sandberg's bluegrass [*Poa secunda*], squirreltail [*Sitanion hystrix*], and six-weeks fescue [*Vulpia octoflora*]) dominate the site; cheatgrass is the main exotic annual (Table 1).

NATIVE GRASS.—This site (T1S, R1W, Sec. 13; elev. 850 m) is <1 km northwest of the unburned big sagebrush site in a former big sagebrush–winterfat community burned by a human-caused wildfire on 26 August 1983. The fire killed the shrubs, and the site was dominated subsequently by native Sandberg's bluegrass, six-weeks fescue, and squirreltail, with

some introduced tumbleweed, cheatgrass, and other exotic annuals present (Table 1).

EXOTIC ANNUALS.—This site (T1S, R1W, Sec. 13; elev. 850 m) is adjacent to the native grass site and was similar to it prior to the 1983 burn (D. L. Quinney, unpublished data). Both sites were burned by the same fire. However, since the fire, the exotic annuals cheatgrass and tumble mustard, with some remnant native grasses, especially Sandberg's bluegrass (Table 1), have dominated the site.

REHABILITATION SEEDING.—This site is located 6 km east, 2.5 km south (T1S, R1E, Sec. 27; elev. 885 m) of the unburned big sagebrush site. The area burned in 1981, was reseeded with desert wheatgrass (*Agropyron desertorum*) in 1982, but burned again in 1983. In 1987 and 1988, the area was dominated by Sandberg's bluegrass, desert wheatgrass, tumbleweed, and other native and exotic forbs (Table 1).

METHODS

To determine the degree of exotic annual invasion at each site, vegetation analysis was conducted in early June 1987 and late May 1988 while Townsend's ground squirrels were being collected. At each site we used a transect with forty 1-m^2 quadrats spaced at 10-m intervals (Daubenmire 1959). Percent cover of each species was estimated using a 1-m^2 quadrat frame divided into tenths to facilitate estimation. To give a better approximation of the availability of each plant species, percent relative cover and percent relative frequency were converted to importance values (Cox 1990).

Squirrels were collected by trapping and shooting at all four sites in May and June 1987 ($n = 75$) and in March and May 1988 ($n = 42$) except from the rehabilitation seeding site in May 1988. Squirrels were aged in the field using pelage and body weight criteria (Bureau of Land Management, unpublished data). Representative specimens were prepared as (1) standard study skins with skulls ($n = 12$), (2) skeletons ($n = 3$), or (3) skulls only ($n = 25$) and deposited in the Albertson College Museum of Natural History. Tooth-wear patterns (Yensen 1991) were consistent with the age assignments for all specimens. Based on these criteria, all 1987 specimens were juveniles since they were collected late in the active season while the adults were entering seasonal torpor; all 1988 specimens were either yearlings or adults.

Stomachs were removed from the animals immediately postmortem and preserved in 70% ethanol. In the lab, stomach contents were removed from ethanol, diluted 50% with water, and homogenized 1 min in a Waring blender to produce fragments of uniform size. The homogenate was washed through a 1-mm sieve (Hansen 1978) and collected in a 0.1-mm screen to remove tiny, unidentifiable fragments. The material was then mounted on microscope slides using Hertwig's and Hoyer's media (Sparks and Malechek 1968).

Plant species in the diet were identified by comparisons to a reference collection of microscope slides using microhistological characters. All reference slides were made from catalogued specimens in the Albertson College Harold M. Tucker Herbarium and were prepared using the technique described above.

For food habits analysis, one slide was examined per stomach. Occurrence of food categories (frequency) was recorded from each of 20 microscope fields per slide using a phase-contrast microscope at 100X. Frequency/20 fields was then converted to percent relative density (Sparks and Malechek 1968) using a table developed for frequency-to-density conversion (Fracker and Brischle 1944).

The importance of each dietary category was calculated in three ways: (1) percent relative density, a standard dry-weight conversion from frequency data (Sparks and Malechek 1968); (2) percent frequency in stomachs, the percentage of stomachs from a site with the item; and (3) percent frequency in microscopic fields, the percentage of all microscopic fields from a site with the item.

Twenty microscopic fields were examined from each slide using a predetermined pattern, and frequency of occurrence of each species was recorded. The frequency of each dietary category/20 fields on one slide was compared with other slides (or replicate counts of the same slide) using the Kulczynski Index (Oosting 1956) (also well known as the Bray-Curtis similarity index [Bray and Curtis 1957]):

$$2w/(a + b)$$

The index was calculated as a dissimilarity index,

$$1 - [2w/(a + b)]$$

using a BASIC microcomputer program provided by Ludwig and Reynolds (1988).

Weather data were from the National Oceanic and Atmospheric Administration monthly

TABLE 2. Late season (25 May–19 June) 1987 Townsend's ground squirrel diets. Data are from stomachs of juvenile TGS at four sites in the Snake River Birds of Prey Area. Adults were entering torpor and none were collected during this period. Dietary composition is given as percent relative density (RD), percent frequency in microscope fields (MF), and percent frequency in stomachs (PS) for each dietary category. Other symbols: + = <1%, – = absent, and *n* = number of stomachs.

	Unburned big sagebrush			Native grasses			Exotic annuals			Rehabilitation seeding		
Dietary category	RD	MF	PS	RD	MF	PS	RD	MF	PS	RD	MF	PS
n		21			20			15			19	
GRASSES												
Bromus tectorum	22	41	71	62	93	100	31	45	87	57	74	95
Poa secunda	24	35	86	+	2	25	7	8	40	+	+	11
Sitanion hystrix	+	2	10	–	–	–	+	+	13	–	–	–
Oryzopsis hymenoides	–	–	–	+	+	5	–	–	–	–	–	–
Grass seed	+	5	19	+	1	5	+	1	13	–	–	–
Grass root?	2	9	10	+	2	5	+	3	13	–	–	–
Total grasses	49			64			39			57		
SHRUBS												
Ceratoides lanata	3	9	52	4	5	10	43	59	67	11	17	32
Artemisia tridentata	+	2	14	1	3	10	6	19	67	+	2	5
Atriplex nuttallii	–	–	–	+	+	5	2	5	13	4	12	37
Chrysothamnus viscidiflorus	–	–	–	–	–	–	–	–	–	+	2	5
Total shrubs	3			5			51			16		
FORBS												
Salsola iberica	39	69	91	3	+	40	1	3	20	7	17	63
Sisymbrium altissimum	+	+	5	5	19	60	–	–	–	2	5	21
Descurainia—2 spp.	+	2	24	+	+	5	–	–	–	–	–	–
Lepidium perfoliatum	–	–	–	2	6	20	+	1	13	1	3	21
Cryptantha interrupta	+	+	5	–	–	–	–	–	–	–	–	–
Ranunculus testiculatus	+	1	5	–	–	–	–	–	–	–	–	–
Lactuca serriola	–	–	–	1	5	25	–	–	–	2	4	5
Chenopodiaceae	–	–	–	+	+	5	+	+	7	+	2	21
Unidentified forb	–	–	–	–	–	–	–	–	–	6	7	11
Total forbs	40			11			2			18		
MISCELLANEOUS												
Insects	8	17	62	19	44	90	7	21	87	3	11	53
Fungi	–	–	–	1	4	10	+	1	7	+	2	5
Unknown	+	+	5	–	–	–	+	4	7	4	5	5
Unidentified seed	+	1	5	+	+	5	–	–	–	–	–	–
Total miscellaneous	8			20			8			8		

Idaho Climatological Data reports for the Kuna 2 NNE weather station ca. 20 km N of the study sites.

RESULTS

Vegetation Analysis

The vegetation at each site (Table 1) varied significantly from the other sites (all $p < .01$; R × C G tests of independence; Sokal and Rohlf 1981). Using the Kuleyznski Index, the similarity among the four sites averaged 48.7% (range 27–73%) in 1987. The unburned sagebrush site was more similar (60%) to the native grass site and less similar to the exotic annual and seeding sites (44 and 47%, respectively).

The vegetation at each of the four sites varied significantly (all $p < .01$; R × C G-tests of independence) between years (Table 1). Importance values averaged 65% similar (range 48–77%) at a site between years. Total percent cover decreased on all sites in 1988. In 1988, when there was less herbaceous cover, the sites were slightly more similar ($\bar{x}$ = 61.3%, range 47–74%). Thus, each site differed almost as much between years as the sites differed among each other in a given year.

Stomach Analyses

Although the three measures of dietary importance (percent relative density [=percent dry weight], percent frequency in microscope fields, percent frequency in stomachs) gave

different numerical results, the rank orders among categories were generally consistent (Tables 2–4). However, percent frequency in stomachs was very sensitive to sample sizes.

There were 1–9 food categories per stomach. Site means varied from 3.8 to 4.4 categories per stomach. The total number of food categories used by all Townsend's ground squirrels sampled at a site varied from 4 to 17 on the three sampling occasions (May–June 1987, March 1988, May 1988). However, if species used in trace amounts (<5% relative density) are eliminated, only 3–6 ($\bar{x} = 4.0$) categories were used per site and only 2–4 species comprised >10% of the diet. Species comprising >10% of the diet at one or more study sites included Sandberg's bluegrass, cheatgrass, six-weeks fescue, winterfat, big sagebrush, tumbleweed, *Descurainia* spp., seeds of bur-buttercup (*Ranunculus testiculatus*), and insects.

Grasses were important constituents of the diet in both 1987 and 1988 and often comprised over 50% of the diet (37–88% relative density, Tables 2–4). Sandberg's bluegrass and cheatgrass were both heavily utilized, especially in March 1988 (55–87% of diet). Late in the Townsend's ground squirrel active season (May and June) use of grasses declined (except at the exotic annual site in 1988). Most of the grass eaten in May–June consisted of seeds, especially of cheatgrass. Sandberg's bluegrass leaves were utilized slightly more than cheatgrass leaves (Tables 2–4), and the two together were far more important than all other grasses combined. Squirreltail was little used, although it was the third most abundant grass.

Winterfat (0–43% relative density) and big sagebrush (0–21%) were both eaten, and winterfat was especially important at the exotic site where it was least abundant. Winterfat was utilized at all sites in 1987, even though it was not abundant enough to be sampled by the vegetation analysis at the exotic annual site. In 1988 it was eaten only at the unburned big sagebrush–winterfat site, and its use declined between March and May 1988 (Table 2). Big sagebrush was used in March at all sites in both years but was less important in May.

Tumbleweed and tumblemustard were the most important forb species consumed. Tansymustards (*Descurainia sophia* and *D. pinnata*), peppergrass, seeds of bur-buttercup, and leaves of prickly lettuce (*Lactuca serriola*) were of secondary importance. All of these are introduced annuals. Bristly cryptantha (*Cryptantha interrupta*) was the only native forb found in Townsend's ground squirrel stomachs. Although 1988 sample sizes were small, the importance of forbs in the diet increased in the samples between March and May 1988, while the percentage of grasses and shrubs decreased (Tables 3–4), thus suggesting large seasonal differences between March and May diets.

A surprising number of insects were eaten, especially in May–June 1987 (3–19%; Table 2). However, insects were not important in 1988 (trace amounts at the big sagebrush site only). Insect remains were so fragmentary that identification was not usually possible. However, abundant Lepidoptera larvae could be recognized by the soft exoskeleton and prolegs, and fragments recognizable as beetle antennae and elytra were found.

The importance values of exotic species were lowest at the unburned big sagebrush site in both years and highest in the exotic annual site in 1987 and at the native grass site in 1988. However, there was no correlation between the importance values of all exotic annuals at a site and their importance in the diet at that site ($r = -.454$; Tables 1–4).

Discussion

The data show that for sites with varying degrees of exotic annual invasion sampled over a two-year period, Townsend's ground squirrels can and do utilize introduced species in their diets, and that cheatgrass, tumbleweed, and tumblemustard are the most important of these.

Both the vegetation at a site and Townsend's ground squirrel diets varied considerably between years and among sites. Differences in amount of precipitation most likely account for the differences in vegetation importance values between years. There was less September–May precipitation (192 mm in 1986–87 and 170 mm in 1987–88 at Kuna ca. 20 km N). The Daubenmire quadrats were taken on the same transect in both years by the same technicians.

The substantial annual differences in Townsend's ground squirrel diets may be the result of (1) vegetation differences between years, (2) the fact that juveniles were sampled in 1987 and adults and yearlings were collected in 1988, (3) differences in collecting dates (25 May–19 June 1987 versus 16–19 May 1988), or (4) small sample sizes.

TABLE 3. Early season (March) 1988 Townsend's ground squirrel diets. Data are from stomachs of adult and yearling TGS at four sites in the Snake River Birds of Prey Area. (Juveniles were not available in March.) Dietary composition is given as percent relative density (RD), percent frequency in microscope fields (MF), and percent frequency of stomachs (PS) containing each dietary category. Other symbols: + = <1%, – = absent, *n* = number of stomachs.

	Unburned big sagebrush			Native grasses			Exotic annuals			Rehabilitation seeding		
Dietary category	RD	MF	PS	RD	MF	PS	RD	MF	PS	RD	MF	PS
n		4			5			7			16	
GRASSES												
Bromus tectorum	39	35	75	67	46	100	51	16	71	39	70	100
Poa secunda	18	73	100	16	92	100	4	86	100	39	71	100
Vulpia octoflora	+	1	25	–	–	–	–	–	–	+	+	6
Sitanion hystrix	–	–	–	–	–	–	+	+	14	–	–	–
Agropyron desertorum	–	–	–	–	–	–	–	–	–	1	1	13
Total grasses	87			83			55			79		
SHRUBS												
Ceratoides lanata	–	–	–	–	–	–	24	55	86	–	–	–
Artemisia tridentata	11	41	50	15	35	60	21	46	100	3	6	13
Atriplex nuttallii	–	–	–	–	–	–	–	–	–	3	8	19
Total shrubs	11			15			45			6		
FORBS												
Salsola iberica	–	–	–	–	–	–	–	–	–	–	–	–
Sisymbrium altissimum	–	–	–	1	5	20	+	1	14	2	4	56
Descurainia—2 spp.	2	6	25	–	–	–	–	–	–	10	25	75
Ranunculus testiculatus	–	–	–	–	–	–	–	–	–	–	–	–
Cryptantha interrupta	–	–	–	–	–	–	–	–	–	2	4	13
Halogeton glomeratus	–	–	–	–	–	–	–	–	–	1	7	13
Lepidium perfoliatum[2]	–	–	–	–	–	–	–	–	–	+	+	6
Crepis acuminata[2]	–	–	–	–	–	–	–	–	–	+	+	6
Lactuca serriola[2]	–	–	–	–	–	–	–	–	–	+	+	6
Chenopodiaceae	–	–	–	–	–	–	–	–	–	+	+	13
Total forbs	2			1			+			15		

The differences in age classes were probably not important. Fitch (1948) found no differences in adult and juvenile diets in California ground squirrels (*S. beecheyi*), nor did Hansen and Johnson (1976) find differences in Wyoming ground squirrel (*S. elegans*) diets by sex or age class. Dyni and Yensen (in preparation) found no dietary differences between adult/yearling and juvenile age classes in Idaho (*S. brunneus*) or Columbian (*S. columbianus*) ground squirrels. On the other hand, the 1988 data do show a strong seasonal component. Thus, the observed annual dietary differences may be a result of later collecting dates in 1987, combined with annual vegetation differences.

Although 117 stomachs were examined, the sample sizes were too small to draw many conclusions about intersite and between-season diets in 1988. This amount of collecting had a deleterious effect on local Townsend's ground squirrel densities, and we recommend use of other methods if seasonal or annual dietary shifts are of interest.

At each site, several plant species were found in Townsend's ground squirrel stomachs that did not appear in the vegetation analysis for that site. The Daubenmire (1959) method of vegetation analysis gave an intuitively acceptable estimate of dominant vegetation, but for establishing a close link between plant abundance and herbivore diets, a finer-scale method of resource analysis is necessary. Since individual Townsend's ground squirrels have large home ranges (mean = 1357 m^2; Smith and Johnson 1985) with a wide foraging radius, it is not surprising that Townsend's ground squirrels were eating species not recorded by the vegetation analysis, even though the sites were relatively homogeneous.

There was no correlation between the total abundance of exotic annuals at a site and their importance in the diet. The number of plant species in the diet not recorded by the vegetation analysis precluded determining dietary preference indices for Townsend's ground squirrels. However, examination of vegetation

TABLE 4. Late season (May) 1988 Townsend's ground squirrel diets. Data are from stomachs of adult and yearling TGS at four sites in the Snake River Birds of Prey Area. Dietary composition is given as percent relative density (RD), percent frequency in microscope fields (MF), and percent frequency of stomachs (PS) containing each dietary category. Other symbols: + = <1%, – = absent, *n* = number of stomachs. Site 1 was not sampled in 1988.

	Unburned big sagebrush			Native grasses			Exotic annuals		
Dietary category	RD	MF	PS	RD	MF	PS	RD	MF	PS
n		1			5			4	
GRASSES									
Poa secunda	2	10	100	19	40	80	–	–	–
Bromus tectorum	22	65	100	35	57	80	24	34	75
Vulpia octoflora	29	75	100	21	36	100	6	18	100
Sitanion hystrix	1	5	100	4	6	40	5	18	50
Agropyron desertorum	1	5	100	–	–	–	–	–	–
Grass seed	2	10	100	4	10	20	2	1	25
Grass root	–	–	–	5	13	60	–	–	–
Total grasses	57			88			37		
SHRUBS									
Ceratoides lanata	–	–	–	–	–	–	13	25	50
Artemisia tridentata	–	–	–	–	–	–	3	8	50
Atriplex nuttallii	3	15	100	6	14	20	2	4	25
Chrysothamnus viscidiflorus	–	–	–	–	–	–	+	1	25
Total shrubs	3			6			18		
FORBS									
Salsola iberica	22	60	100	–	–	–	–	–	–
Sisymbrium altissimum	–	–	–	6	18	60	1	4	75
Descurainia—2 spp.	–	–	–	–	–	–	15	33	50
Ranunculus testiculatus	17	55	100	–	–	–	28	43	50
Forb root	–	–	–	+	1	20	–	–	–
Total forbs	39			6			44		
MISCELLANEOUS									
Insect	–	–	–	–	–	–	+	1	25
Unknown	–	–	–	–	–	–	+	7	25
Total miscellaneous	0			0			+		

abundance (Table 1) in comparison to consumption (Tables 2–4) indicates that most of the abundant plant species were also important in the diet, and that rare plants were being used only in trace amounts. There were some interesting exceptions to this, however. Cheatgrass was dietarily important (39% relative density) but not recorded in the vegetation analysis at the rehabilitation site.

Diets became more diverse in May, probably as a result of grasses curing and seeds becoming available. Ground squirrels eat large amounts of seeds prior to entering torpor (Rickart 1982, E. Yensen, personal observation). Perhaps if insufficient seeds are available during a drought year, Townsend's ground squirrels turn to insects as a fat source. However, at the exotic annual site where insect use was highest in 1987, cheatgrass (mostly seeds) was the major constituent of the diet. This relationship should be explored further.

Although halogeton (*Halogeton glomeratus*) was not recorded by the vegetation analysis, small amounts of it were found in two stomachs at the rehabilitation site in March 1988 (Table 3). Halogeton is poisonous to livestock, but sheep can eat it with impunity in winter, probably because rains have leached the oxalates out of the dried leaves (Cook 1977). Presumably, Townsend's ground squirrels were eating dried, rather than fresh, leaves in March.

Idaho and Columbian ground squirrels have highly varied diets of 11–25 plant species per fecal pellet group (Dyni and Yensen, in preparation). However, in that study only 2–4 plant species (usually grasses) contributed >10% to the diet. Rogers and Gano (1980) found that only three plant species (*Poa* spp., *Descurainia pinnata*, and *Lupinus laxiflorus*) contributed >10% of the diet of Townsend's ground squirrels in southeastern Washington. Hansen and Ueckert (1970) found 1–5 species contributed >10% in the diverse (47 plant species) diets of

Wyoming ground squirrels in Colorado. Hansen and Johnson (1976:750) concluded that

> Richardson[=Wyoming] ground squirrels graze on a variety of plants as they fill their stomachs rather than selecting only preferred foods when their stomachs are nearly empty. This may be an evolutionary strategy developed to allow them to consume vetches. The dilution of toxic foods by non-toxic foods decreases the probability of plant poisoning.

Freeland and Janzen (1974) reviewed strategies of herbivory by mammals in response to secondary plant compounds. They suggested that a generalist herbivore should feed predominantly on one or two foods, but continue to sample other foods present. When an herbivore experiences a nutritional deficiency, it should sample all available foods until it finds something which supplies that nutrient.

The feeding strategies proposed by Freeland and Janzen (1974) and Hansen and Johnson (1976) appear to occur in several members of the subgenus *Spermophilus*. The data indicate that ground squirrels specialize on 2–4 highly nutritional species, but supplement them with a wide variety of other species, apparently as "poisoning insurance." In this study, Townsend's ground squirrels similarly depended on only a few species for the bulk of the diet, but a wide variety of trace species was not available. If any of these species should provide insufficient quantities of a key nutrient (e.g., linoleic acid necessary for hibernation), then the limited selection of food species could have negative population consequences.

The question of whether Townsend's ground squirrels can utilize exotic annuals as dietary staples is answered in the affirmative by this study. Native forb species were of minor importance in the diet, but this does not necessarily reflect preference. Native forbs are now so rare at the four sites that none were recorded by the vegetation analysis, and thus they may not have been available for consumption. Only one native forb (*Cryptantha*) was found in the stomachs. The consequences of limited dietary variety on the long-term nutrition of Townsend's ground squirrels are unknown.

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LITERATURE CITED

ALCORN, J. R. 1940. Life history notes on the Piute ground squirrel. Journal of Mammalogy 21: 160–170.

BRAY, J. R., and J. T. CURTIS. 1957. An ordination of the upland forest communities of southern Wisconsin. Ecological Monographs 27: 325–349.

COOK, C. W. 1977. Effects of season and intensity of use on desert vegetation. Utah Agricultural Experiment Station Bulletin 483, Utah State University, Logan. 57 pp.

COX, G. W. 1990. Laboratory manual of general ecology. 6th ed. Wm. C. Brown Publishers, Dubuque, Iowa. 251 pp.

DAUBENMIRE, R. F. 1959. A canopy-coverage method of vegetation analysis. Northwest Science 33: 43–66.

DAVIS, W. B. 1939. The Recent mammals of Idaho. Caxton Printers, Ltd., Caldwell, Idaho. 400 pp.

FITCH, H. S. 1948. Ecology of the California ground squirrel on grazing lands. American Midland Naturalist 90: 334–340.

FRACKER, S. B., and J. A. BRISCOE. 1944. Measuring the local distribution of *Ribes*. Ecology 25: 283–303.

FREELAND, W. J., and D. H. JANZEN. 1974. Strategies in herbivory by mammals: the role of plant secondary compounds. American Naturalist 108: 269–289.

HANSEN, R. M. 1978. Shasta ground sloth food habits, Rampart Cave, Arizona. Paleobiology 4: 302–319.

HANSEN, R. M., and M. K. JOHNSON. 1976. Stomach content weight and food selection by Richardson ground squirrels. Journal of Mammalogy 57: 749–751.

HANSEN, R. M., and D. N. UECKERT. 1970. Dietary similarity of some primary consumers. Ecology 51: 640–648.

HOWELL, A. H. 1938. Revision of the North American ground squirrels, with a classification of North American Sciuridae. North American Fauna 56: 1–256.

JOHNSON, D. R. 1961. The food habits of rodents on rangelands of southern Idaho. Ecology 42: 407–410.

JOHNSON, D. R., G. W. SMITH, R. M. OLSON. 1977. Population ecology and habitat requirements of Townsend ground squirrels. Pages 203–225 *in* Snake River Birds of Prey Research Project, Annual Report, 1976.

JOHNSON, M. K. 1980. Food of Townsend ground squirrels on the Arid Land Ecology Reserve (Washington). Great Basin Naturalist 37: 128.

KOCHERT, M. N., and M. PELLANT. 1986. Multiple use in the Snake River Birds of Prey Area. Rangelands 8: 217–220.

LUDWIG, J. A., and J. F. REYNOLDS. 1988. Statistical ecology. John Wiley & Sons, New York.

OOSTING, H. J. 1956. The study of plant communities. 2nd ed. W. W. Freeman, San Francisco.

RICKART, E. A. 1982. Annual cycles of activity and body composition in *Spermophilus townsendii mollis*. Canadian Journal of Zoology 60: 3298–3306.

ROGERS, L. E., and K. A. GANO. 1980. Townsend ground squirrel diets in the shrub-steppe of southcentral Washington. Journal of Range Management 33: 463–465.

SMITH, G. W., and D. R. JOHNSON. 1985. Demography of a Townsend ground squirrel population in southwestern Idaho. Ecology 66: 171–178.

SOKAL, R. R., and F. J. ROHLF. 1981. Biometry. 2nd ed. W. H. Freeman & Co., San Francisco. 859 pp.

SPARKS, D. R., and J. C. MALECHEK. 1968. Estimating percentage dry weight in diets using a microscopic technique. Journal of Range Management 21: 264–265.

U.S. DEPARTMENT OF INTERIOR. 1979. Snake River Birds of Prey. Special Research Report. U.S. Bureau of Land Management, Boise District, Boise, Idaho. 142 pp.

YENSEN, D. L. 1980. A grazing history of southwestern Idaho with emphasis on the Snake River Birds of Prey Area. Progress Report. U.S. Department of Interior, Bureau of Land Management, Boise, Idaho. 82 pp.

YENSEN, E. 1991. Taxonomy and distribution of the Idaho ground squirrel, *Spermophilus brunneus*. Journal of Mammalogy 72: 583–600.

YENSEN, E., D. L. QUINNEY, K. JOHNSON, K. TIMMERMAN, and K. STEENHOF. 1992. Townsend's ground squirrel population fluctuations in southwestern Idaho. American Midland Naturalist. In press.

YOUNG, J. A., R. A. EVANS, R. E. ECKERT, JR., and B. L. KAY. 1987. Cheatgrass. Rangelands 9: 266–270.

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